Evolutionary progression and breakdown of sociality in insects(昆虫における社会性の発達と崩壊)

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論文内容の要旨

The aim of the study

To be cooperative or to be selfish, which is more adaptive on your situation? The evolution of cooperation is one of the most interested topics for evolutionary biology (Wilson and Hölldobler, 2005; Nowak, 2006; West et *al.*, 2007). Social behavior evolves in many taxa of animals (Axelrod, 1984; West *et al.*, 2005, 2006) and especially insect sociality shows tremendous variety (Wilson, 1971; Choe and Crespi, 1997). Cooperation means that selfish replicators forgo some of their reproductive potential to help one another. Cooperaters indirectly increase the frequency of their own alleles by increasing the reproduction of related individual (Hamilton, 1964). By contrast, cheating is evolved from the sociality for the selfish strategy (Bourke, 1991; Turillazzi *et al.*, 2000). Selfish individuals cheat cooperator and increase their fitness without taking part in altruistic work for organization. There are various causes for evolution of these selfish strategies such as sex-ratio manipulation, green-beard genes, conditional use of sex, and even clonal males (Keller and Ross, 1998; Pearcy *et al.* 2004, Fournier *et al.* 2005; Ohkawara *et al.* 2006).

Numerous empirical data and theoretical hypotheses have tried to reveal the rule for the evolution of cooperation or cheating, but it is still difficult to arrive at a conclusion. Here, I add two impressive examples from novel view point. Examinations were conducted with the materials which are at the halfway of the evolution between cooperative and selfish. One of these materials is the stag beetle, *Figulus binodulus*. Stag beetles are generally fire-eating insects which have exaggerate weapon to secure limited resource, but *F. binodulus* represents cooperative traits such as brood caring. This example showed undergoing shift from being selfish to being cooperative. As the other material, parthenogenetic ant *Pristomyrmex punctatus* gives us the potential of the way to social breakdown. The ants have managed well developed social system, however *P. punctatus* includes cheaters which are quite workless and excess selfish reproduction. This case revealed an opposite pattern against the stag beetle, the shift from being cooperative to being selfish. Examination of the undergoing evolution would extract the essential points for the mechanisms of social evolution. This study must provide a novel viewpoint in comparisons with the cases treating social systems already evolved to an extreme stage.

Outline of the thesis

In Chapter 2, I focused on the social evolution the stag beetle. Rigorous environments are likely to induce social behaviour in insects. This condition may lead to sociality, even in the stag beetle. The aim of this study is to show that sociality has evolved instead of fighting, a contrasting strategy, within a related species group in a similar environmental condition. The Asian stag beetle *Figulus binodulus* provides an excellent system to examine the social behaviour of the stag beetles. *F. binodulus* has a small body size and no sexual dimorphism. Adults of *F. binodulus* found a colony and reproduce under the bark of dead wood. They crush the wood during the period of growing their offspring. Hatched larvae eat such sawdust and accomplish the whole growth stage with their parents. Three series of experiments were examined for this stag beetle in Chapter 2. First, the effects of association behaviour on the growth of offspring are investigated in *F. binodulus*. Next, how parental care affects the offspring's growth is examined, and the validity of the hypothesis that parental care is advantageous for the offspring of *F. binodulus* is tested. Additionally, the relationship between kin recognition and social behavior is examined. The final body length of broods growing with adults was significantly larger than those growing with no adults. When sawdust was artificially digested, the growth rate of larvae improved. Mortality of the juveniles was higher for offspring growing with unrelated adults than those with related adult beetles. These findings suggest that *Figulus binodulus* improves the food for their larvae, and that the sociality of this species has evolved for adaptation against poor resource conditions. Moreover, the larvae can receive benefits from every adult, whereas adults may recognize their relatives more strictly than unrelated offspring. Sociality in the stag beetle is very rare case. Sociality in the stag beetle may be an alternative strategy for small species instead of fighting.

In Chapter 3 and 4, I attended to the evolution of social parasitism in the ant. Social parasitism is the cheating strategy which evolves from social system. Usual haplodiploid system in Hymenoptera takes genetic conflict between the workers, thus causes mutual policing to suppress the less related descendant. But the conflict does not work in the situation of parthenogenetic reproduction of female (thelytoky). The thelytokous reproduction can be one of remarkable trigger for social parasitic evolution. The parthenogenetic ant *Pristomyrmex punctatus* represent unique life history characteristics. This is a queenless ant species so that all workers

reproduce by thelytoky in their youth and later shift to cooperative behaviours. In spite of cooperative characteristics of normal (S-type) workers, unusual large morphological (L-type) workers do not work at all except for reproduction. Genetic distinction between L-type and S-type workers represent a lineage specialized for cheating. In Chapter 3, Molecular phylogeny between the large workers was estimated in *P. punctatus* including the L-type workers discovered from 9 sites. The analysis represented that L-type workers evolved independently at least two times within the species. Additionally, cooperater-cheater relationship represented two genetic patterns. In Chapter 4, Behavioral similarity was compared between the L-type workers which belong to the different genetic clades. Both L-type workers represented similar social parasitic behaviors. However, there are several differences in the morphological and behavioral peculiarities, suggesting that parasiting strategies between these L types workers are slightly different. These findings revealed the parallel evolution of selfish cheater within the species. Thelytokous reproduction is advantage with the high demographic potential, but can be the hot bed of evolution of cheaters.

論文審査結果の要旨

本博士論文は、社会性の発達の中間段階に位置する昆虫を材料として、社会性の発達ないし維持のメカニズムを明らかにすることを目的として行われた研究の成果である。

まず、朽木中にて集団で生活するチビクワガタに注目し、その飼育実験および行動実験を通して、チビクワガタに血縁認識が存在すること、また成虫が集団でコロニーの幼虫に資源を供給することを示した。クワガタムシ類で亜社会性が存在する可能性は従来から指摘されてきたが、それを実証したのは本論文が最初である。そして朽木という限られた特異な資源利用が、チビクワガタのような利他的な種と、社会性を持たない攻撃的な利己的タイプの一般的なクワガタムシの分化をもたらしたと結論した。

次に本論文では多女王制というユニークな社会性をもつアミメアリに注目し、その社会を崩壊にまねくような社会寄生が進化するメカニズムの解明を試みた。アミメアリには大型のL-typeと呼ばれる個体がまれに出現するが、本論文では日本各地に広くこのタイプが出現するコロニーがあることを見出した。行動解析の結果、このL-typeはコロニー内のほかのワーカーの労働に依存する社会寄生タイプであることが示された。

ミトコンドリアDNAを用いた分子系統解析の結果、本土のアミメアリは大きく2つの系統からなることが示されたが、この社会寄生はいずれの系統にも存在していた。この結果から、社会寄生は少なくとも2回、独立に進化したことが推定された。これは社会寄生が近縁な系統から進化するとするエメリー則を支持する結果である。

さらに本論文では、社会寄生の維持機構として、寄生タイプ間の闘争がその増殖率を抑制し、結果としてコロニーを崩壊させるような社会寄生の増えすぎが抑えられるのではないか、という仮説を提唱し、行動解析により実証した。この仮説は従来の考えとは異なるユニークなものであり、社会寄生の維持機構を考える上で重要な発見である。

以上のように本論文は利己性と利他性の進化のメカニズムを、社会性の発達の中間段階に注目することで解明することに成功した。本論文の成果は極めてユニークなものであり、高い意義をもつ。以上の成果は森英章君が自立して研究活動を行うに必要な高度の研究能力と学識を有することを示している。従って森英章君提出の論文は，博士（生命科学）の博士論文として合格と認める。